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Flowering in a Ponderosa Pine Provenance Plantation in Eastern Nebraska

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Nebraska plantation ponderosa pines from 50 provenances exhibited variations in flower sex, northern sources producing predominately ovulate strobili and southern sources predominately staminate. Relative proportions of ovulate and staminate strobili produced appear to be influenced by photoperiod length as expressed by differences between latitudes of seed origin and plantation location.

Keywords: *Pinus ponderosa*, seed sources, flowering strobili

MANAGEMENT IMPLICATIONS

Results of this study on flowering are useful for seed collectors, trees breeders, and those involved in establishing seed orchards of ponderosa pine in the central Plains. If production of relatively large quantities of both ovulate and staminate strobili is desired at any early age, the selection of seed sources should be from native stands in north-central Nebraska or east-central Montana. Seed sources from these areas have been among the fastest growing in most provenance plantations established throughout the Plains area.

INTRODUCTION

Flowering at an early age is an important trait in tree selection for breeding programs. Little information on this trait is available for the eastern range of ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.). Past observations in eastern Nebraska indicate that planted ponderosa pine usually begins flowering later than certain origins of jack pine (*P. banksiana* Lamb.) and Scots

pine (*P. sylvestris* L.), which can produce abundant pollen and conelets at 4 to 6 years of age.² Flowering at 8 years field age is the average for ponderosa pine according to Wang (1977), but Righter (1939) observed staminate flowering at 2 years and ovulate flowering at 4 years on var. *ponderosa* at Placerville, Calif.; he observed strobili at 5 years on var. *scopulorum*.

To obtain data on flowering, a 13-year-old provenance plantation of ponderosa pine was studied in 1978 at the University of Nebraska's Horning State Farm, in eastern Nebraska. Some flowering had been observed in this plantation as early as 1973, at age 8 years. Observations of the plantation in early spring 1978 indicated copious flowering for the first time. Accordingly, in 1978, the frequency and quantity of ovulate and staminate strobili production were determined for each seed source in the plantation.

MATERIAL AND METHODS

The 8-acre plantation was established April 1968 with 2 + 1 seedling transplants of 50 well-distributed provenances (fig. 1) of ponderosa pine. Forty-seven sources are var. *scopulorum* of eastern range natural stands, known as Rocky Mountain ponderosa pine; the other three sources are var. *ponderosa* from western Mon-

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²Where an age is mentioned, it is total age from seed, unless the term "field age" is used.

tana. The plantation, one of many in a regional study of genetic variation, was established primarily to evaluate resistance to the needle blight fungus *Dothistroma pini*.

The experimental layout consists of 10-tree, linear plots of each seed source, with six replicates. Spacing between trees is 8 feet (2.4 m) within rows and 13 feet (4.0 m) between rows. The plantation is at 41.0° N. latitude, 95.9° W. longitude, at an elevation of 1,100 feet (330 m), on a west-facing slope of deep, silt loam soil derived from loess. The growing season averages 170 days. Mean annual precipitation is 30 inches (76 cm).

Weeds were controlled from 1968 through 1972 by mowing between rows and by applying herbicide spray in early spring along both sides of tree rows. Maintenance since 1972 has involved periodic mowing only. In early summer of 1976 and 1977, the trees were sprayed with an insecticide to reduce the effect of tip moth (*Rhyacionia bushnelli* Busck), which was interfering with the disease research objectives.

During mid-May of 1978, the rating system described below was used to evaluate flowering on each tree in the plantation, once to count ovulate strobili, and again to count clusters of staminate strobili. In ponderosa pine, ovulate strobili are usually produced in the upper crown, where 1 to 4 of them may occur at the terminal of each elongating branch. Staminate strobili usually cluster at the base of new growth on lateral branches, in lower and middle crown. The rating system equated a cluster of staminate strobili to one ovulate strobilus.

The occasional solitary staminate strobilus was counted if it was the only evidence of flowering on a tree. The rating system for quantity of flowering was as follows:

Flowering	Number of strobili	Rating
None	0	0
Light	1-10	1
Medium	11-20	2
Heavy	≥21	3

Tabulations were made of the number and percent of trees in each seed source (1) bearing strobili of either or both sexes, (2) with ovulate strobili, and (3) with staminate strobili. Quantity of flowering (ovulate, staminate, and total) was expressed as a percent of the plantation mean after average tree ratings for each seed source were calculated. Correlations of flowering with seed source mean tree heights and with latitude and elevation of seed sources were investigated.

In late April 1982, one replication of the same plantation was reexamined to see if the flowering pattern was still the same or had changed.

RESULTS

Flowering data are arranged by eight geographic areas, so that geographic area means can readily be compared (table 1). Within each area, sources performed similarly in regard to total flower production and distribution of staminate and ovulate flowers. These areas are similar to the clusters derived from nursery seedling analyses of these same seed sources (Read 1980).

Percent of Trees Flowering

Sixty-five percent of all trees had flowers of either or both sexes (table 1) while 35% had no flowers. Differences in flowering among the geographic areas were readily apparent (table 1, fig. 1). Percent of flowering trees was generally highest among sources from Montana and the central Plains. Flowering was least among sources from higher elevations in the central Rocky Mountains and among most sources from the southern Rocky Mountains.

Seed sources with the highest percent of trees flowering were 720 and 721 from the Niobrara River area in northern Nebraska; 852 and 853 from the Pine Ridge of northwestern Nebraska; and 819 from the Bitterroot Valley of Montana. Seed sources with the lowest percent of trees flowering were 766 and 869 of southern New Mexico and Arizona, and 848 and 857 from the central Rocky Mountains in southern Wyoming.

Distribution of Flowering by Sex

The 1,920 flowering trees comprised 3 groups: 40% produced male and female strobili, 32% produced female strobili only, and 28% produced male strobili

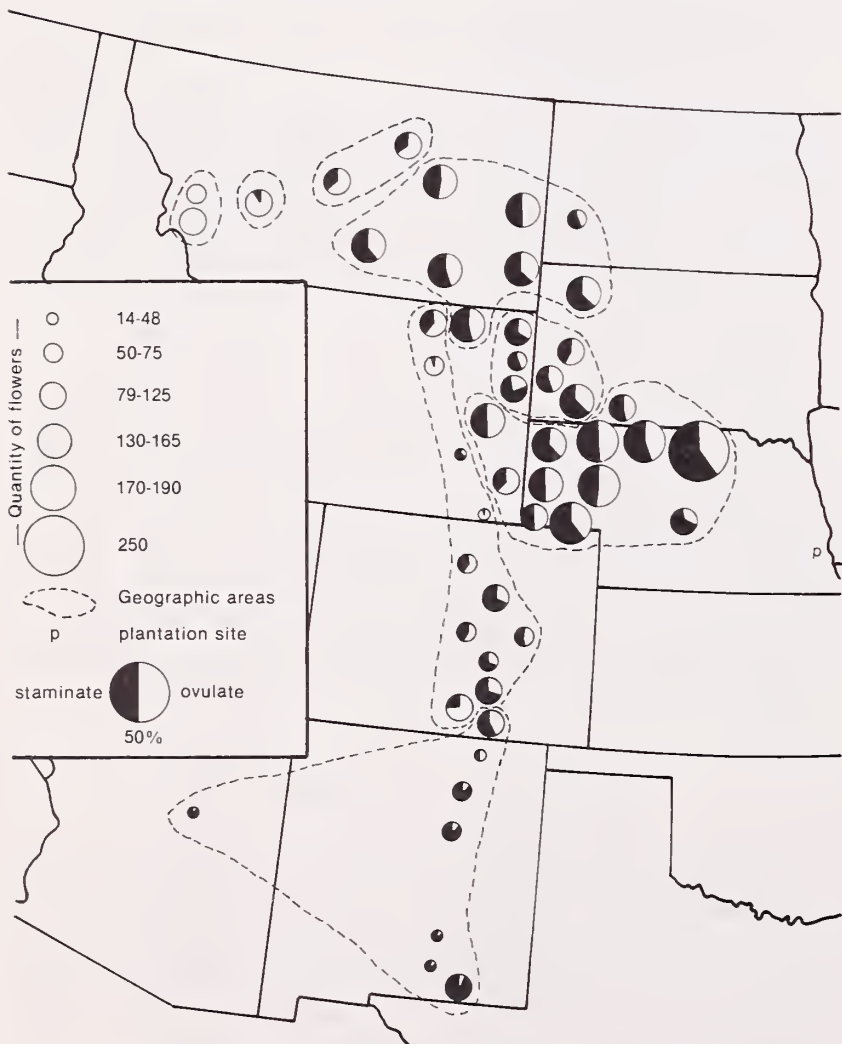


Figure 1.—Quantity of flowering and percent distribution by sex, by seed sources. Seed sources are grouped into geographic areas.

Table 1.—Location data of seed sources, 13-year tree heights, and flowering data of ponderosa pine by seed sources in an eastern Nebraska provenance plantation

Geographic area	Source number	State	Latitude	Elevation	13-year height (as percent of plantation \bar{x})	Total trees	Trees' with strobili	Trees' with ♀ strobili	Trees' with ♂ strobili	Quantity of flowering ² (as percent of plantation \bar{x})			
										Ovulate	Staminate	Total	
					<i>feet</i>								
						<i>number</i>	-----		<i>percent</i>				
<i>var. ponderosa</i>													
Bitterroot Valley	819	Mont.	45.9	4100	105	59	90	90	0	189	0	88	
	820	Mont.	46.2	4500	98	57	79	79	0	121	0	57	
	Area mean \bar{x}					102		84	84	0	155	0	73
Transition	816	Mont.	46.6	4500	108	60	80	80	8	185	13	97	
<i>var. scopulorum</i>													
North-central Montana	813	Mont.	47.9	4700	91	61	64	57	25	111	56	82	
	815	Mont.	47.1	4800	102	59	61	53	34	113	61	86	
	Area mean \bar{x}					97		63	55	29	112	58	84
Northern Plains	811	Mont.	47.6	2900	112	60	83	75	57	169	135	151	
	826	Mont.	47.0	2750	105	60	75	67	60	152	130	141	
	702	N. Dak.	46.9	2500	101	60	47	30	30	63	66	64	
	822	Mont.	46.2	3800	119	60	83	57	72	121	165	144	
	824	Mont.	45.9	3400	110	60	73	60	63	139	141	140	
	827	Mont.	45.8	3800	108	61	77	46	66	98	144	122	
	704	S. Dak.	45.6	3450	102	57	77	53	68	117	168	144	
	832	Wyo.	44.9	3900	106	60	78	58	57	127	125	126	
Area mean \bar{x}					108		74	56	59	123	134	129	
Black Hills	833	Wyo.	44.6	4000	104	59	64	37	58	75	134	107	
	834	Wyo.	44.4	5500	94	57	49	28	35	50	70	61	
	835	Wyo.	43.9	5080	101	59	49	20	44	38	111	77	
	837	S. Dak.	44.3	6300	98	59	78	69	46	136	90	111	
	838	S. Dak.	43.9	5680	94	58	64	52	48	111	115	113	
	840	S. Dak.	43.7	4200	106	59	75	47	68	101	152	128	
Area mean \bar{x}					100		63	42	50	85	112	100	
Central Plains	849	Wyo.	43.0	5200	100	59	76	64	51	133	120	126	
	851	Nebr.	42.7	4200	101	60	77	47	65	104	161	134	
	852	Nebr.	42.5	3800	104	60	90	77	68	185	151	167	
	853	Nebr.	42.9	3600	108	60	90	77	65	170	159	164	
	854	S. Dak.	43.2	3300	106	59	66	49	51	105	113	109	
	721	Nebr.	42.9	2700	115	61	85	74	67	168	177	173	
	720	Nebr.	42.7	2300	116	60	98	82	93	199	260	232	
	856	Nebr.	41.4	2900	98	58	67	38	62	76	140	110	
	846	Wyo.	42.2	4200	98	56	66	64	38	168	83	123	
	845	Nebr.	41.5	5100	91	60	68	50	42	98	89	93	
	723	Nebr.	41.8	4600	101	59	81	63	59	139	130	134	
	758	Nebr.	41.2	4500	101	60	83	57	77	125	196	163	
	Area mean \bar{x}					103		79	62	61	139	148	144
	Central Rocky Mountains	829	Wyo.	44.8	5100	94	59	66	56	34	117	69	91
831		Wyo.	44.2	5800	87	60	57	57	3	101	3	49	
848		Wyo.	42.6	6900	87	59	36	20	29	37	153	45	
857		Wyo.	41.2	7700	80	57	40	39	4	77	4	38	
760		Colo.	40.2	8400	74	59	54	39	25	70	41	54	
859		Colo.	39.4	6500	91	55	62	31	51	63	116	91	
762		Colo.	39.4	5900	96	59	53	32	31	63	64	63	
763		Colo.	39.1	7800	90	61	56	44	23	83	56	69	
860		Colo.	38.6	6500	88	55	49	25	31	39	72	57	
861		Colo.	37.9	6600	94	59	71	29	63	67	132	102	
764	Colo.	37.9	8800	98	60	65	65	15	119	33	73		
Area mean \bar{x}					89		55	40	29	76	68	67	
Southern Rocky Mountains	765	Colo.	37.3	7000	106	61	70	39	59	92	118	106	
	862	N. Mex.	37.0	7350	91	58	47	31	24	48	45	46	
	863	N. Mex.	35.8	6400	104	59	46	12	46	17	90	56	
	864	N. Mex.	35.5	6400	96	56	45	5	45	13	88	53	
	869	Ariz.	35.2	7000	104	50	30	4	28	5	58	33	
	766	N. Mex.	33.3	7300	101	53	13	2	13	7	22	15	
	767	N. Mex.	33.0	6400	104	54	44	6	43	11	73	44	
	768	N. Mex.	32.2	5800	106	60	57	7	57	10	141	79	
Area mean \bar{x}					102		45	14	40	25	79	56	
Plantation totals						2931							
Plantation means						100	65	47	44	100	100	100	
						(12.8 feet)			(0.84)	(0.96)	(1.80)		

¹Percent of trees with ovulate strobili plus percent of trees with staminate strobili may exceed percent of trees with strobili because many flowering trees had both sexes of strobili.

²Quantity of flowering is expressed by summing all individual tree ratings (0, 1, 2, 3), dividing by the number of trees and arriving at an average tree rating for each source. Ovulate, staminate, and total flowering is expressed as a percent of plantation mean. Plantation average tree ratings are in parentheses.

only. Thus, 60% of flowering trees produced only one sex of strobili at age 13. Of the trees containing ovulate strobili, only 21% were rated as flowering heavily, while 35% rated medium, and 44% light flowering. Of the trees containing staminate strobili, 48% were rated as flowering heavily, 20% medium, and 32% light.

Flowering categorized by sex of the strobili was strikingly different among geographic areas (table 1, fig. 1). Ovulate flowering was predominant on the var. *ponderosa* sources from the Bitterroot Valley of Montana; sources 819 and 820 were exclusively ovulate, and the Transition source 816 was high in ovulate but low in staminate flowers. Ovulate flowering was moderate to heavy on most other Montana sources and on sources of the Niobrara River area of northern Nebraska. Ovulate flowering was generally low on most central Rocky Mountain sources, and very low on all southern Rocky Mountain sources.

In contrast, staminate flowering was lacking or very light on five seed sources of western and north-central Montana. The central Rocky Mountain sources, moderately low in ovulate flowering, were also very low in staminate flowering. All southern Rocky Mountain sources produced more staminate than ovulate strobili. The highest percent of trees with staminate strobili came from sources of the central Plains in Nebraska, and some sources in the northern Plains of Montana.

Quantity of Flowering

The total quantity of flowering as expressed by the average of all individually rated trees, yielded a plantation mean of 1.80. The average ovulate (0.84) and staminate (0.96) ratings per tree were similar (table 1). Quantities of flowering for each seed source (ovulate, staminate, and total), expressed as a percent of the plantation mean, are shown in the last three columns of table 1.

The differences in total quantity of flowering among the geographic areas were large (table 1, fig. 1). The 12 central Plains sources averaged 144% of the plantation mean, with source 720 of northern Nebraska bearing the maximum number (232% of the plantation mean) of both ovulate and staminate strobili. The northern Plains sources of eastern Montana also bore high numbers of strobili. Generally, lowest strobili production was in seed sources from the central and southern Rocky Mountains (67% and 56% of the plantation mean, respectively).

Correlations

Simple correlation coefficients between flowering data, tree heights, and two place-of-origin items are shown in table 2.

Tree Height and Seed Source Elevation

The average 13-year heights of trees in the plantation were negatively correlated with elevation of seed

source ($r = -0.66$). Although this effect has been observed in provenance tests of some species, particularly in the western United States, Wright (1976) maintains that consistent elevational trends are generally lacking in provenance tests.

Flowering and Tree Heights

Percent of trees flowering was correlated with tree height ($r = 0.51$); seed sources having the tallest trees had the highest percent of flowering trees. Sources with the shortest trees had the lowest percent of flowering trees (table 1). For example, seed source 720 from Ainsworth, Nebr., which was the second tallest (116% of plantation mean or 14.9 feet), had the highest percent (98%) of trees flowering. At the other extreme seed source 857 from Buford, Wyo., which was the second shortest (80% of plantation mean or 10.3 feet), had only 40% of trees flowering (table 1).

Total quantity of flowering compared with seed source mean height produced an even higher correlation ($r = 0.63$, table 2). Although the percent of flowering trees and total quantity of flowering correlated reasonably well with mean heights, which, as noted above, were negatively correlated with seed source elevations, the quantity of ovulate and staminate flowering was distributed differently. Percent of trees with staminate strobili and quantity of staminate strobili were correlated with mean tree height ($r = 0.56$ and 0.59 , respectively), but percent of trees with ovulate strobili and quantity of ovulate strobili were not as highly correlated with mean heights ($r = 0.31$ and 0.40 , respectively).

The major deviations in the correlations of flowering with tree height were the New Mexico and one Arizona seed sources which had low percentages and quantities of flowering, yet were above average in mean heights.

Flowering and Seed Source Elevation

All flowering traits were negatively correlated with seed source elevation, which, as noted previously, was negatively correlated with 13-year mean height. Total quantity of ovulate and staminate strobili was the most highly correlated flowering trait with seed source elevation ($r = -0.72$, table 2). Maximum quantities of flower production were mainly in seed sources from elevations less than 5,000 feet (1,524 m). At higher elevations, there was a wide range of flowering; but in general there was less flowering in the high elevation seed sources.

Flowering and Seed Source Latitude

Percent of trees flowering was correlated with seed source latitude ($r = 0.56$, table 2). Southern and central Rocky Mountain sources had the lowest percent of trees flowering, 45% and 55%, respectively. Only 13% of the trees in source 766 Ruidoso, N. Mex. had flowered. The highest flowering percentages were in sources from the central and northern Plains and the Bitterroot Valley of Montana. Five northwestern





Table 2.—Simple correlation coefficients¹ (*r*) between flowering data and tree heights, and seed origin elevation and latitude

Item	13-year height	Seed origin	
		Elevation	Latitude
13-year height	-----	-0.66***	0.20
Percent trees flowering	0.51***	-0.64***	0.56***
Percent trees w/♀	0.31*	-0.53***	0.70***
Percent trees w/♂	0.56***	-0.52***	0.07
Quantity ♀	0.40**	-0.59***	0.67***
Quantity ♂	0.59***	-0.58***	0.11
Total quantity ♀ + ♂	0.63***	-0.72***	0.45***

¹Level of significance: 0.05 = *
0.01 = **
0.001 = ***

Nebraska sources from approximately 42° latitude, had a combined average of 89% of trees flowering (table 1).

Total quantity of flowering was not as highly correlated with seed source latitude ($r = 0.45$, table 2). The greatest quantity of flowering was in central Plains sources, and the next greatest quantity was in northern Plains sources. Southern latitude sources flowered least. Although central Rocky Mountain sources range in latitude from 38° to 45°, most of those sources were rated low to moderate in flowering.

The percent of trees with ovulate strobili and the quantity of ovulate flowering were highly correlated with seed source latitude (table 2). Staminate flowering, however, showed no correlation with the latitude of seed source.

Correlations between flowering and seed source latitudes would have been higher had the confounding effect of varying elevations not been present.

DISCUSSION AND CONCLUSIONS

These results are further evidence of strongly inherited traits in eastern range ponderosa pine populations. Climatic factors that vary with elevation and latitude of seed source are important in determining the range of genetic differences in height growth and flowering. These become apparent when these sources are grown together under uniform environmental conditions.

Because the plantation is at 1,100 feet elevation, all 50 seed sources are growing at an elevation considerably lower than that of the natural stands from which the seeds were collected. The major effect of these differences in elevation appears to be in the rate of tree growth and, consequently, in the total quantity of flowering as influenced by tree size. Most, although not all, low elevation sources were fast growers (tallest trees). The exceptions indicate that certain seed sources are not generally programmed to grow fast, even under favorable environmental conditions.

The relationship of flowering to latitude is somewhat different. The northern sources from Montana, which are adapted to longer day lengths at 46° to 48° latitude, now grow under shorter day lengths at 41° latitude. Conversely, the southern sources from new Mexico and Arizona, adapted to shorter day lengths at 32° to 37° latitude, now grow under longer day lengths at 41° latitude.

Mirov's (1956) observations indicated that flowering of pines was not affected by change in day length when various species, including ponderosa, were moved from their native habitat to Placerville, Calif. Mirov (1967) later concluded that pines appear to be neutral with respect to flowering and length of photoperiod.

Giertych (1967), however, states that short days promote ovulate flowering and long days promote staminate flowering in pines. This is in agreement with results of the present study. The northern seed sources from Montana, which now experience shorter days in the Nebraska plantation, are predominantly ovulate flowering, whereas the southern seed sources from New Mexico and Arizona, which now experience longer days in the Nebraska plantation, are higher in proportion of staminate flowering. This phenomenon was also observed with acorn squash and cucumber, monoecious plants, with promotion of male flowers under long days and female flowers under short days (Nitsch et al. 1952). Pharis et al. (1975) suggest that photoperiod possibly controls the endogenous concentration of gibberellin, influencing the effective level of auxin, which in turn determines the sex of flowers.

The flowering patterns observed in this study should not be considered unusual. Wright (1953) states that young eastern white pines (*Pinus strobus* L.) generally produce ovulate strobili almost exclusively for many years, whereas Korean pines (*Pinus koraiensis* Sieb. and Zucc.) have predominantly staminate strobili when young. Wright reported that in Scots pines some trees were predominantly staminate while others were predominantly ovulate. Thus, similar flowering pat-

terns have been noted in other species of pines for several years after flowering begins.

Finally, a reexamination of one replication of the same plantation during late April 1982 indicated that the sexual orientation of the flowering pattern observed in 1978 is still present. Although total flowering per tree has increased, the trees from northern seed sources still produced almost exclusively ovulate flowers while trees from southern seed sources produced predominately staminate flowers.

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